PARALLEL ECOGENOTYPICAL
COLOR VARIATION
IN BUTTERFLIES [1]

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A STUDY OF THE GEOGRAPHICAL VARIATION within many species of butterflies in the western parts of North America has led to the discovery of many parallelisms in the color variation within these different species. Mere chance alone as the cause of this phenomenon was not considered probable as the parallelisms were found to be of great quantity and to present astounding regularities in geographical variation. After a study of the different environments in which the various species lived and of the pigment types most likely to be found under various environmental conditions, it was found possible to make a correlation between the pigment color variation and the environmental variation. It is with this correlation that the present paper is primarily concerned.

THE COLORS OF NORTH AMERICAN BUTTERFLIES

As a basis for making a correlation between pigment color variation and the environmental conditions, it is necessary to consider briefly the pigments and color patterns of the butterfly wings themselves. It will be unnecessary to go into much detail as recent reviews on the chemistry and physiology of the pigments (Wigglesworth, '39 and Lederer, '40) cover all the modern and accepted work in the field, and Goldschmidt's recent review ('38) of the experimental work on Lepidopteran patterns gives a general picture of the problems involved in their physiological and genetical determination. All that is necessary here is a brief outline of the various pigment groups in the various systematic divisions of the butterflies. Thus, each pigment group rather than each species may be handled together in correlations with the ecological factors of the environment.

The color of the butterfly wing, or of any part of it, is essentially the summation of the color of the individual scales

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[1] *The ecological part of this paper was presented at the winter meetings of the Ecological Society of America in Philadelphia, Dec. 1940. Abstract published, Hovanitz ('40c).*

on the wing; however, each scale is just beyond the resolving power of the human eye when in place on the wing membrane,[2] and the colors, therefore, appear as uniform suffusions on the wing surface. The pattern is the result of the differential distribution of the different colored scales on the wing membrane. In ordinary description, the butterfly wing is said to consist of a ground color, a pattern color and smaller amounts of other colors. The ground color, in the sense that is most often used and in the sense that I shall use it here, is any color which covers the greater part of the wing other than that occupied by the pattern elements. The pattern color is the dark color which forms the pattern bands or spots on the wing; in cases where the bands fuse or where the entire wing is overlaid with the "pattern" color, the ground color in the above sense does not exist. This pattern color belongs to the melanin group of pigments which are normally black in the butterflies but vary also to brown and gray. Few other pigments of butterflies are known as well, chemically. The yellow pigment of the Pieridae has received more attention than most others (see Lederer) and is classed as a pterine. Because the chemical classification of butterfly pigments is still in an immature stage of development, and though homologies between the pigments of various species or families would be highly useful, these unfortunately cannot be made at the present time on such a basis. Pigments will therefore be grouped into classes on the basis of (1) their visible color similarity, (2) their presence in the same species or closely related species and (3) their similarities in variation under the influence of similar environmental conditions. The following classes of partially homologous and partially analogous colors have, therefore, been arranged for use in this paper (excluding some minor colors of no interest here):

Group 1.—The black, dusty brown and gray colors which form the pattern elements, black spots and "melanic suffusion" pigment in nearly all species of butterflies. These are the melanin pigments.

Group 2.—The tawny, rufous, "red," "orange," and "yellow"

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[2] *The body of the butterfly is colored as well as the wings. This coloring is not only due to scales but also to hairs. These hairs receive in ontogeny the same pigments as the scales on the wing and, therefore, form a color pattern as well. On account of the similarity and because of the ease of working with the colors spread out on a flat surface, the wing colors alone will be discussed in this paper; it will be assumed that the body colors vary simultaneously.*

colors with a brown tint which form the ground color in the Nymphalidae, Riodinidae, Satyridae, Lyeaenidae, Danaidae, and Libytheidae; also in this group is placed the yellow and white pigment found in the above families. For no other reason than for similarity of variation, these latter are placed here. They do not seem to be homologous with the yellows and whites (pterines) of the pierids and papilionids below, though the restricted orange and red spots of the latter two families are placed here.

Group 3.—The yellow, orange, and white ground color pigments of the families Pieridae and Papilionidae. The chemical classification of the pigments of this group in the Pieridae is known (they are the pterines mentioned above). The Papilionid pigments appear to be unknown chemically but are nevertheless put in this class because of similarity in color and variation with the pierid pigments.

The darkness or lightness of the wing is determined by the quality and quantity of pigments upon it and these are determined by the interaction of the various pigments. The pattern pigments of *Group One* are normally darkest of all the three groups; an increase in the area covered by this pigment would, therefore, give a darker wing. As the ground color pigments of *Groups Two* and *Three* are usually lighter in color than those of *One*, an increase in the area covered by those pigments would give a lighter colored wing. The relation of *Group One* to *Groups Two* and *Three* is therefore one of presence and absence; increase of *Group One* must be made at the expense of *Groups Two* and *Three* if the wing remains the same size. There are several ways in which the pigments of *Group One* can cover more wing area: the width of each part of the pattern may widen, the wing may be overlaid by a melanin pigment (scattered individual scales) in whole or in part, or the pattern itself may be changed by the addition of some element which was absent in the reduced condition. Goldschmidt ('38) lists the known effects of mutant genes of these types in the Lepidoptera. In considering darkness or lightness of the melanin pigments of *Group One* in this paper, no distinction will be made between these different gene and physiological reactions; the distinction between increase or decrease (or "darkness" and "lightness") of *Group One* as a whole, only, will be considered. The phylogenetic relationships involved in the various pigment changes will be left for future and more detailed papers. In the butter-

flies of North America, the melanin pigment itself varies but slightly in color within a species; it is invariably black and so for simplicity such variation will be disregarded in this paper.

Group Two contains a heterogeneous series of partly non-homologous pigments varying in color from white to dark rufous or tawny; for this reason, it is more difficult to analyze in terms of increase or decrease and presence or absence. Each particular pigment not only varies in area of wing covered but also its character within an area. Three main and apparently homologous types or subgroups of these *Group Two* pigments may be utilized for description: (*a*) The tawny, rufous or "red-brown" pigment which is the commonest ground color of the families listed above under this group. This pigment varies in color from a very dark rufous or tawny to a very light "faded" shade that in some groups is almost white. It is not known whether this variation is due to a chemical pigment change such as oxidation or reduction, or merely to increase or decrease in the amount of pigment deposited in the scale per unit area. In some species, a red pigment which appears to be homologous with this rufous or tawny is present (*Melitaea phaeton*); it varies from dark red to light yellow-brown and it seems most probable that a chemical change is here the factor involved. (*b*) The yellow pigments of the families above listed. This color is only of minor importance since it does not very often cover an area of more than merely spots or bands upon the wing. In a few varieties, it does assume the status of being the main ground color, however. The variation in color of this pigment is from yellow to white, due probably to a reduction in the amount of pigment deposited per unit area in the scales. (*c*) The orange and red pigments which form the border spots of the Pieridae and the Papilionidae (central spots of *Parnassius*). These are the orange and red tips of *Anthocharis*, the border spots (not the central band) of yellow or red in *Papilio* and the central yellow or red spots in *Parnassius*. They vary in a way similar to the pigments of (*a*) and (*b*) above and may prove to be chemically homologous with them. They vary not only in size but also in tint, having a continuous range of variation from yellow to red.

Group Three is much simpler to analyze than the above two. The white, yellow and orange ground-color pigments of the Pieridae and the Papilionidae are placed here. These three colors generally maintain three discrete units rather than continuous

series of variation in most cases. The butterfly's wing color may be all white (leucopterine), all yellow (xanthopterine) or all orange or red (erythropterine). Only in a few populations do modifying genetic factors seem to blur the discreteness of these three. It may be that these three pigments are merely oxidation products of the pterines which are deposited in the wings at different stages of their development. Since the order of deposition of the pigments appears almost never to be anything other than white-yellow-orange rather than white-orange-yellow or some other combination, this theory seems somewhat plausible.

CORRELATION OF COLOR VARIATION AND
ENVIRONMENTAL VARIATION

The method employed in determining the exact environmental factor to correlate with the pigment variation often brings up difficult problems and one cannot always attribute a given color variant to a single factor. To an ecologist this is not surprising. A living organism is in a world of interacting factors, many of which can hardly be separated from one another for analysis. In many cases, however, a single factor may be a limiting one and where this is true it is relatively simple to discover it. In order to get a rather accurate analysis, it is necessary to know as much as possible of the geographical distribution of the species studied, of its variation within as well as between populations, of the seasonal variation in species (if any), of those areas of the color pattern which are most likely to be first affected by changed environmental conditions, of the interbreeding habits of the populations studied so as to guard against error in properly separating non-interbreeding units, and a good field and meteorological knowledge of the annual climatic fluctuations throughout the range of the species, together with as much life-history data to go with this as possible. The extent to which one's correlations are correct is directly proportional to the extent to which the above factors are known. Fortunately (as will be discussed in more detail later), along the Pacific Coast certain peculiarities in the distribution of the physical factors of the environment have rendered this study invaluable aid in simplifying the correlations to be made. The following correlations were found to take place between the three pigment groups of butterflies and the environmental conditions: In the *Group*

One pigment, there is increased quantity (area and intensity on the wing) in the following regions or under the following conditions. In the *Group Two* pigments, there is an intensification or darkening of the pigments of the three subgroups and in the case of subgroup (*c*) an increase in area covered on the wing in the following regions and under the following conditions. In the *Group Three* pigments, there is often increased development of the lighter of the three pterine pigments (white, yellow and orange) in the following regions and under the following conditions.

1. In the north as compared to the south
(in the northern hemisphere)

Polar regions (northern regions in the northern hemisphere) have a reduced annual as well as seasonal quantity of solar radiation even though summer days are longer in these regions than in equatorial regions (Kimball and Hand, '36). Intensity of light is therefore less in the north than in the south. As heat upon the surface of the earth is dependent mainly upon solar radiation, cooler weather is the rule in the north and warmer weather in the south. Moisture and precipitation are usually not so dependent upon differences in solar radiation; however, available moisture may be. Water which is frozen is unavailable to plants and animals. Precipitation in the far north may be in the form of snow and remain as ice upon the earth. A given amount of precipitation in the south may, therefore, be of more importance than the same amount in the north. In considering these factors in relation to color variation later, many micro-ecological factors must be taken into account, too. A species which in the north lives on the south-facing slopes of a hill may obtain more than or as much solar radiation as the same species in the south where it may live on the north-facing slopes. Another factor which is of importance in comparing northern and southern areas is the available time interval during the year which is suitable for growth. In the north, the long, cold winters are unfavorable for life, and cold-blooded animals, at least, must hibernate. In an animal which has but one brood per year, the rate of development must be more rapid in the north than it need be in the south. Summary: In the north as compared to the south, there is in general less light, less heat, often less available moisture and less time available for growth.

2. *At lower elevations as contrasted with*
higher elevations at the same latitude

Many complicating conditions arise in comparing lower elevations with higher elevations. Lower elevations have a lesser intensity of solar radiation than higher elevations (Kimball and Hand, '36). Lower elevations have a more humid atmosphere than higher elevations because of the water loss due to decreased atmospheric pressure and consequent lower temperature in the latter, even though there may be less precipitation in the former. Precipitation at increase in elevation becomes correspondingly less available because of the decrease in temperature. Higher elevations allow for a shorter available growing season for living things because of the colder seasonal and annual temperatures. The interaction of these factors do not always form a readily obvious ecological arrangement. As mentioned above, the interactions and effects must be considered on a micro-climatic basis as well as on such general terms as they are here being discussed. The time of year when these factors are critical to the organism must always be considered. Summary: At lower elevations, there is a lesser intensity of solar radiation, which is shown as a decrease in light intensity and direct heat; there is a higher air temperature and more atmospheric humidity though the annual precipitation may be lower. There is a longer available growing season per year.

3. *In areas having a dense vegetative cover*
as contrasted with desert or desert-like areas
having little vegetative cover

In areas having a denser vegetative cover, one must consider the indirect effects of this vegetation in causing microclimatic conditions as well as the direct ones. High solar radiation, high temperatures, high precipitation and high humidity are favorable to vegetative life. If edaphic and extreme conditions are not considered, the amount of vegetation in a given region is fairly directly proportional to the relative amounts of these factors present and available to the plants. One effect of greater vegetative cover on solar radiation is that it tends to reduce the amount reaching the surface of the earth or reflected back into the atmosphere by absorbing it in the green leaves, by absorption in the more humid atmosphere and in the clouds which pro-
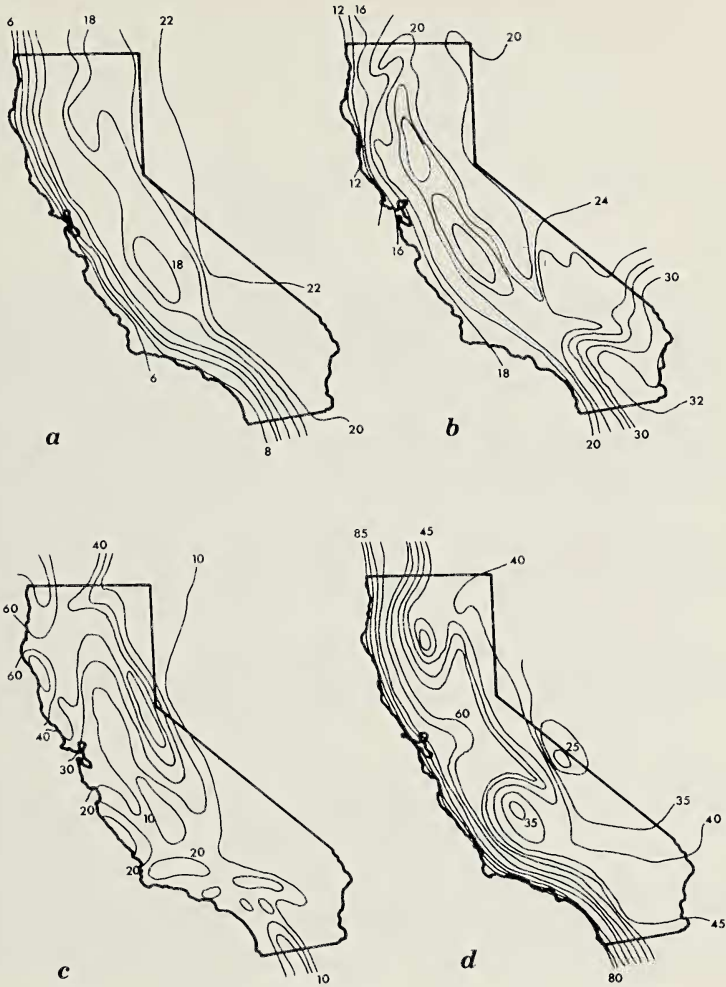
Fig. 1.—Series of maps of California illustrating the variation in climatic factors by meteorological data. (*a*) Mean annual range of temperature (°C.). Note the remarkably reduced range of temperature variation on the coast and the increased range inland. This is of importance in that the long period of favorable temperatures at the coast allows time for a lengthened development rate whereas the reduced favorable season inland makes necessary a fast development rate. Compare with map showing color races. (*b*) Average temperature in July (°C.). Note the increased temperatures inland and the decreased temperatures on the coast as well as the gradient from north to south. (*c*) Mean annual rainfall (inches). Note the increased rainfall on the coast and to the north as compared with decrease inland and to the south. Also increased rainfall on the western side of the mountain ranges and decrease on the eastern rain-shadow side. (*d*) Average relative humidity in July (%). Note the higher humidity to the north and especially along the coast and the extreme aridity of the valleys cut off from the

coast. (*e*) July daytime cloudiness (Tenths). Note the increased cloudiness in the northwest as compared with the southeast. (*f*) Showing by shaded lines the position of the most important mountain systems of California and by arrows the direction of increase of solar radiation in general throughout the state. Since solar radiation intensity is greatest in equatorial as compared with polar regions, the arrows should point directly southward. However, on account of increased cloudiness and humidity in the coastal areas (which absorb radiation) as compared with inland areas, the arrows have deviated eastward. Solar radiation intensity increases also in elevation in the mountain ranges but this could not be shown here. [Data for (*a*) to (*e*) after Brooks, Connor, and others ('37) by courtesy of the Harvard University Press.]
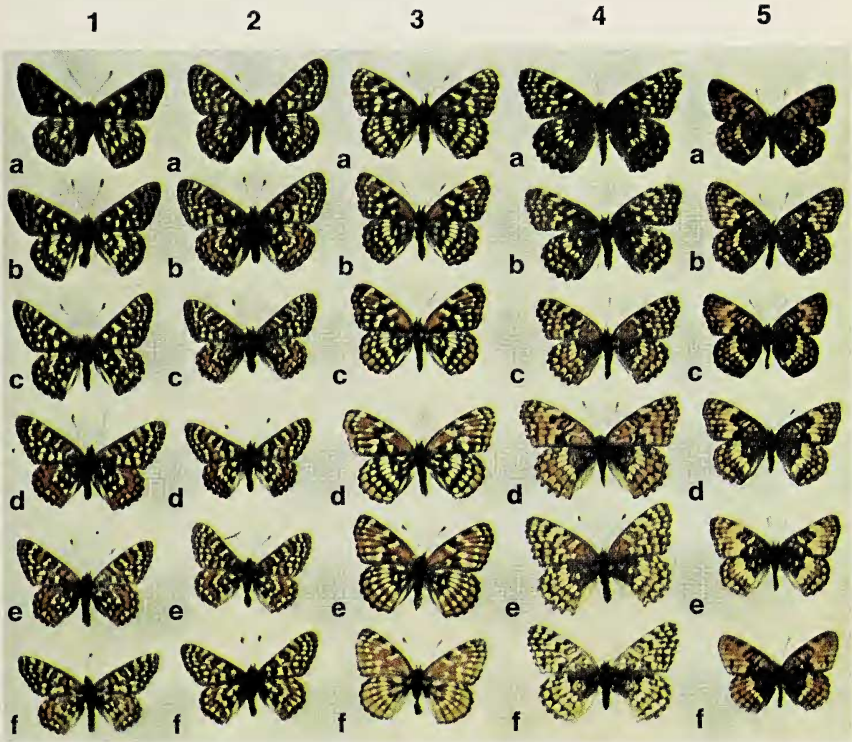
Fig. 2.—Geographical variation in five species of *Melitaea* in California and southern Oregon. (1) *M. chalcedona* (or *phaetona* section), (2) *M. editha*, (3) *M. leanira*, (4) *M. palla* and (5) *M. hoffmanni*. The order of variation from *a* to *f* is from those having the most melanin (*Group One*) pigment deposition on the wings, having the red, rufous, or tawny coloration (*Group 2-a*) the darkest and the yellow pigments (*Group 2-b*) the darkest to the butterflies having the reverse of this type of pigmentation. The darkest black shown is melanin. The grays are the rufous pigments and the whites represent the white or yellow pigment. Each specimen is used to show the type of pigmentation present at a given area on the map (Fig. 3) and should be used in conjunction with it. The specimens are intended to show only the relative amounts of the pigments present in the different geographic races and are not intended to be accurate in detail throughout the considered area concerning pattern variation details.

Fig. 3.—Map showing the distribution of *Melitaea* in California and southern Oregon. The numbers and letters (1*a*, 3*b*, 5*d*, etc.) represent approximate areas where populations of butterflies live having the characteristics in color of the specimen of the same designation as shown in figure 2. Comparisons should be made with that figure. The dash-dot line encloses the central valley of California where no Melitaea has been known to exist.
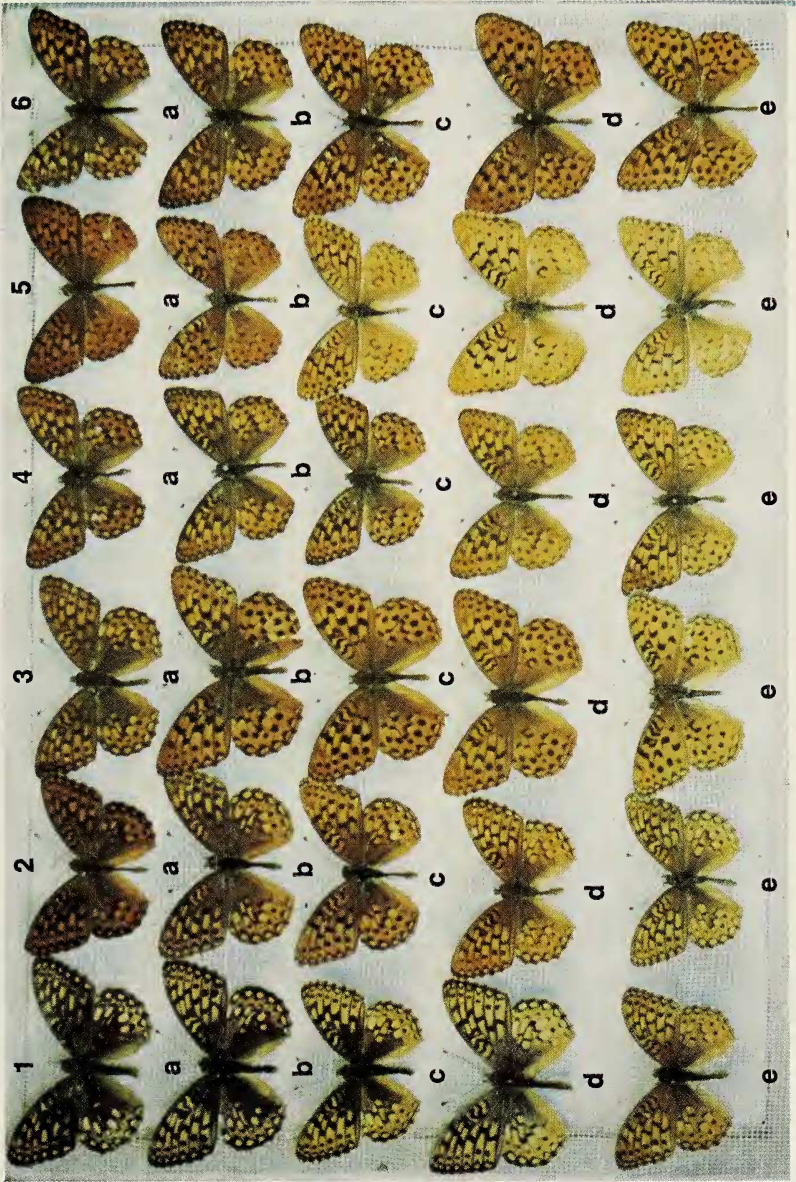
Fig. 4.—Geographical variation in five species of *Argynnis* in California. (1) *Argynnis callippe* (Coast Range cline), (2) *A. callippe* (Sierra Nevada cline), (3) *A. monticola*, (4) *A. montivaga*, (5) *A. adiaste*, (6) *A. zerene*. The ground color of the specimens figured is tawny, varying from dark at (*a*) to light at (*e*). The black pattern is melanin (*Group One*) which is most extensive at (*a*) and least extensive at (*e*). This figure should be used in conjunction with the map (fig. 5) as the numbers and letters thereon refer to the specimens shown in this figure.

Fig. 5.—Map showing the distribution of the five species of *Argynnis* in California. The numbers and letters represent approximate areas where populations of butterflies live having the characteristics of the specimen of the same designation on figure 4. The dash-dot line encloses the central valley of California and excludes the Mohave desert area where no *Argynnis* have ever been found.
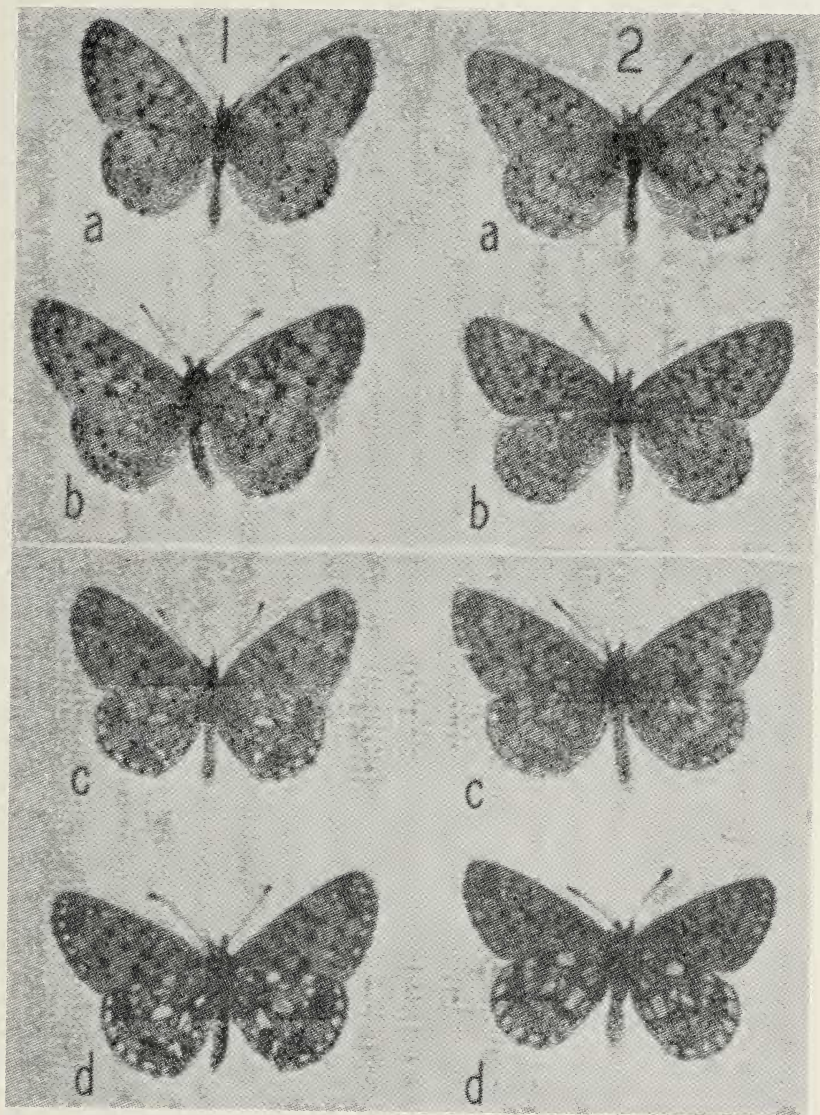
Fig. 6.—Variation in two species of *Argynnis* (*Brenthis*). 1*a*, *Argynnis selene* dorsal surface from Colorado; 1*b*, same from Newfoundland; 1*c*, same specimen as 1*a* but ventral surface; 1*d*, same specimen as 1*b* but ventral surface. 2*a*, *A. aphirape* dorsal surface from Colorado; 2*b*, same from Labrador; 2*c*, same specimen as 1*a* but ventral surface; 2*d*, same specimen as 2*b* but ventral surface.
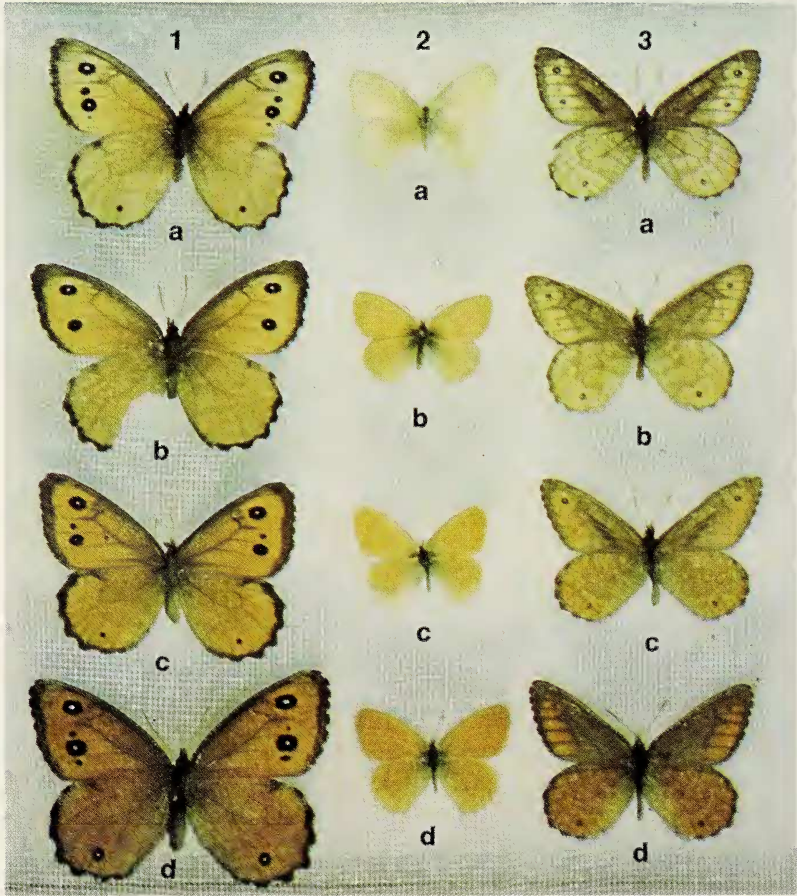
Fig. 7.—Parallel variation in the ground color of the Satyridae. 1. *Oeneis nevadensis,* 2. *Coenonympha tiphon,* 3. *Oeneis chryxus.* Specimens from (*a*) to (*d*) vary from a white ground color through yellow-brown to dark orange-brown. See text for distribution.
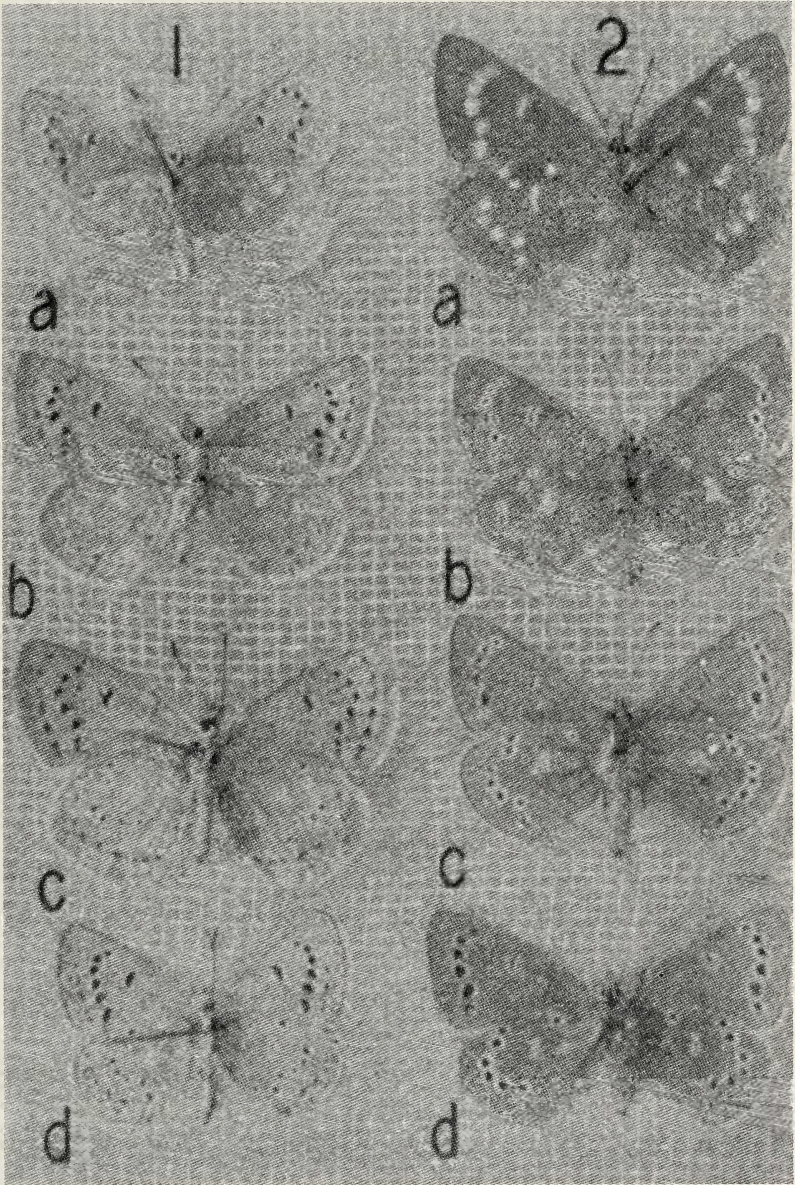
Fig. 8.—Variation in size of melanic spots in the Lycaenidae. 1. *Plebejus icarioides*, 2. *Glaucopsyche lygdamus*. See text for distribution.
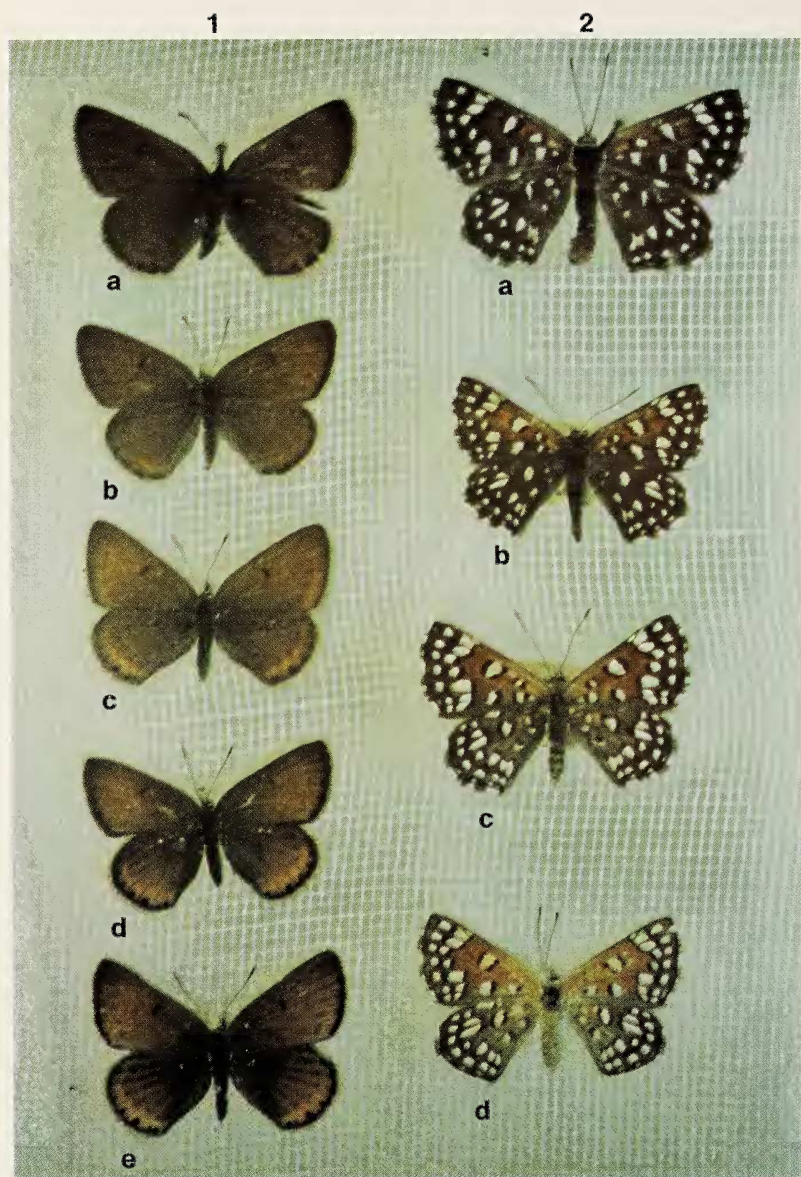
Fig. 9.—Variation in the color of the Lycaenidae and the Riodinidae. 1. *Plebejus saepiolus,* upper surface of females from California. Letters *a* through *e* refer to localities on the map (fig. 9). 2. *Apodemia mormo,* upper surface, showing increase in melanin (*Group One*) pigmentation and darkened *Group Two* pigmentation at the top and the reverse at the bottom.

duce the precipitation. Thus the relative amounts of these factors available to the insect may be greatly reduced by the vegetation itself (Popp and Brown, '36). Desert vegetation, being a gray or pale green color and with but few leaves, would also be less effective in absorbing radiation; more would, therefore, reach the surface of the earth or be reflected back, into the atmosphere. Soils in regions where there is a greater quantity of vegetative cover are usually darker in color than soils in desert areas because of the increased plant humus in the former. Such dark soils would therefore absorb more solar radiation than the light desert soils. Temperatures in areas of good vegetation are likely to be less extreme during the normal growing season of the plants because vegetation can stand little freezing temperatures; also the evaporation of water from the plants or surroundings tends to cool the immediate vicinity. On account of this more median temperature relation, the available growth period for the organism would be longer. Summary: In areas of denser vegetation, there would usually be greater humidity, greater precipitation and more cloudy days, less solar radiation (direct or reflected) and consequently less light and direct heat, and more median temperatures at least during the growing season of the year. Available development period would be longer.

4. In areas where the atmosphere is foggy, smoky or dusty as contrasted with areas where the sky is clear

In areas where the atmosphere is cloudy, foggy, dusty or smoky more solar radiation would be absorbed before it reached the earth, or would be reflected back into the atmosphere than in areas where the atmosphere is perfectly clear and clean (Kimball and Hand, '36 and Brackett, '36). Also, in areas where clouds or fog occur there is usually a denser vegetative cover and the consequent effects of this have been discussed above. Since less solar radiation is received at the surface of the earth under these conditions, the temperature will be lowered. As seen in the cool, foggy coasts and islands, and the hot deserts (Russell, '26), this is of considerable importance where the area is large enough (air mass movements play a large part in the general temperature regulations, however). Smoke and dust over the industrial regions play a large role in the amount of solar radiation reaching the earth (Brackett, '36), by decreasing the amount and also seem to have an effect in producing more fog

and precipitation. Summary: Material in the atmosphere such as clouds, fog, dust and smoke will decrease the amount of light received at the surface of the earth, will tend to lower the temperature and may increase the humidity and precipitation.

5. In areas of dark colored ground cover (plants or soil) as contrasted with areas having light colored ground cover

Dark colored ground cover such as dark rock, soil or plant cover has been discussed in reference to the effects of plants above (3). Smaller or larger areas of dark rock cover some regions of the earth (see Benson, '33, and Hovanitz, '40a) and these tend to absorb more solar radiation while areas of light colored rock (such as white granite or sand dunes) will reflect a large part of the radiation striking it. In the latter case, the radiation striking an object between the sky and the earth will therefore be increased. Snow and ice may be considered as a ground cover here, too. The effects of the soil color on temperature may be slight but dark rock will absorb more heat than a light rock and on that account will be warmer. Summary: Areas of dark colored ground cover will favor an absorption of more solar radiation and an object between the sky and the earth will therefore receive less light than if the ground cover was light colored and reflected more. In the case of a dark rock cover the temperature may be raised but as given above (3), if the dark ground cover is due to vegetation, the temperature may be lowered. There is probably no effect on humidity or precipitation or upon available time for growth except in the effect of the vegetation.

6. In areas of greater precipitation as contrasted with areas of greater aridity

In areas of greater precipitation, several factors interact to produce different effects. In order to have rain, there must be clouds. Increase in clouds is followed by decreased solar radiation; this means less light and less heat. Increase in moisture is usually accompanied by increase in vegetation; the effects of this are mentioned above (3). Increase in precipitation is often followed by increase in humidity; this absorbs light and heat which might otherwise reach the earth. Summary: Greater precipitation may be accompanied by indirect decrease in solar radiation and this is reflected in less light and less heat. The

direct effect of more water for the organism must also be mentioned as well as the usually greater humidity of the air in these regions.

7. *In coastal or insular areas as contrasted with inland areas*

In coastal areas, the effect of proximity to a large body of water in cases where the winds are not always from land to sea is to create a higher humidity of the air. The direct effect of this higher humidity is to absorb a portion of the solar radiation; the result, of course, is less light and less heat reaching the earth. The closer an area is to the coast, the greater is the · amount of radiation absorbed. The effects of this on climatic zones can be clearly seen by reference to the map of the climates of California by Russell ('26), and life zones of California by Grinnell ('35) or the maps given in this paper (fig. 1). The increased humidity of the air is also of great importance to the existence of plant life since water loss from the leaves by transpiration would not be so great. The indirect effects of greater vegetative cover would come in here again (3). Another indirect effect of the proximity to a large body of water is the relatively smaller amplitude of seasonal variations in temperature (Brooks, Connor, and others, '37); this would allow animals a much longer available period of growth in these areas. Summary: In coastal areas, solar radiation is reduced and consequently light and heat received at the earth's surface are less. Available development time for organisms is increased because of the more even distribution of temperature during the year.

8. *In seasonally dimorphic forms: In those seasons of the year in which any of the above conditions might be seasonally restricted, or in the spring or autumn*

Seasonal variations in the environment comparable to the regional ones considered above also occur. Cooler seasons of the year in a region of high annual temperatures may be comparable to the warm season of the year in a region of low annual temperatures. The wet season of the year in a semi-arid region may be comparable to a region where the entire year is wet. In spring and autumn as compared to summer there is a diminished intensity of solar radiation (Brackett, '36); this results in less light and less heat reaching the earth. Precipitation is perhaps

unaffected though available moisture may be as decreased evaporation from the soil (less solar radiation) will tend to raise the water table. Summary: Seasonal variations in the climate may be comparable to the regional ones discussed above. In spring and autumn, there is less light and less heat received at the surface of the earth, other things being equal. Precipitation and humidity are perhaps not affected.

The following table gives a recapitulation of the summaries of the eight regions or conditions above.

It is seen from this summary that if all the other conditions remain constant, light will be decreased in each of the regions or under the conditions stated; available moisture and humidity will be increased in five, neutral in two or three and may be decreased in one; temperature will be decreased in six and neutral in two; available growth period will be longer in five, shorter in one and neutral in two. It would seem that light intensity is of great importance in affecting butterfly coloration and that the other three factors may also be of equal or nearly equal importance. Under natural conditions these factors do not always vary in a parallel way but at such times, one or more may prove to be of primary importance to the organism. In some localities, different factors may affect the different species because of their different life-cycle arrangement, thus giving the effect of nonparallel variation. This may be true of such places as the Atlantic coast where increase in humidity and available moisture is southward in summer instead of northward as on the Pacific coast (Brooks, Connor, and others, '36). The result is a balance between light intensity, moisture, temperature and available period of development which at times gives a decidedly non-parallel-appearing distribution of color variation. But, along the Pacific coast, the factors seem to vary in almost perfect unison (fig. 1). Light intensity decreases to the north, precipitation and humidity increases to the north and temperature is lower to the north. With such a unity in the environmental factors, it is no wonder that the colors in even distantly related species show an extremely parallel range of variation in this region. In the extreme polar regions, *Group One* and *Two* pigments become decreased and in *Group Three*, the darker pigments become increased presumably because the short period available as a growing season is there the limiting factor.

	1. Polar areas	2. Lower elevations	3. Greater vegetative cover	4. Foreign substances or fog in atmosphere	5. Dark ground cover	6. Increase in precipitation	7. Coastal areas	8. Spring and autumn
LIGHT	decrease	decrease	decrease	decrease	decrease	decrease	decrease	decrease
AVAILABLE MOISTURE AND HUMIDITY	decrease or same[3]	increase	increase	increase	same[4]	increase	increase	same[5]
TEMPERATURE	decrease	increase or decrease[6]	decrease	decrease	increase or decrease[7]	decrease	decrease	decrease
AVAILABLE GROWTH PERIOD	shorter	longer	longer	longer	same[8]	longer	longer	same
PIGMENTS OF GROUP ONE AND TWO	darker	darker	darker	darker	darker	darker	darker	darker
PIGMENTS OF GROUP THREE	lighter	lighter	lighter	lighter	lighter	lighter	lighter	lighter

[3] Possibly decrease because if part of water is frozen, available water is less.

[4] If vegetative cover is the cause of the dark ground cover, the available water and moisture would be increased through the indirect effects of the vegetation.

[5] Available moisture may be increased due to the lesser evaporation of water from the soil and the consequent rise in the water table. Of importance at least in the semi-arid regions of coastal California.

[6] At lower elevations, the amount of direct heat received from the sun is less but due to the higher atmospheric pressure and the basin phenomena of valley areas, the air temperature will be higher.

[7] If the dark ground color is due to the nature of the rock cover, the temperature will tend to increase. If due to vegetative cover, the temperature will decrease.

[8] If the dark ground color is due to vegetation, the available growth period may be increased (see 3). If due to the rock cover, it might also be increased in cold regions due to the greater heat absorption though decreased in hot, dry regions due to the excessive evaporation.

EVIDENCE FOR THE CORRELATION BETWEEN
THE COLOR VARIATION AND THE
ENVIRONMENTAL VARIATION

For lack of space, it will be impossible to cover the variation of all species of butterflies; instead, a few selected examples which will illustrate all three types of color change (*Groups One, Two* and *Three*) in relation to the environment will be given here. Excellent climatic maps to accompany the distributional maps of the butterflies given herein will be found in Grinnell's Life Zone Map of California ('35), Russell's Climates of California ('26) and Brook's, Connor's and others' Climatic Maps of North America ('36). Correlation can also be made with the very generalized maps of California accompanying this paper (fig. 1).

Butterflies Having Pigments of Groups One and Two Only

Family Nymphalidae. — The illustrations (fig. 2) show a series of each of the five variable species of the genus *Melitaea* in California and southern Oregon. These species as numbered on the illustration are: (1) *chalcedona* (a representative of *phaeton*), (2) *editha*, (3) *leanira*, (4) *palla* and (5) *hoffmanni*.[9] The pigments shown are of *Groups One* and *Two*, and the parallelism in their variation is easy to observe. The darkest black color shown is melanin (*Group One*); the next lightest shade of gray represents the red, rufous and yellow-brown pigment of subgroup *a* of *Group Two*; and the lightest color is the yellow-white color of subgroup *b* of *Group Two*. It is seen that *Group One* is most extensive at the top (*a*) and least extensive at the bottom (*f*), and that *Group Two* is least extensive but darker at the top (*a*) and most extensive and lightest at the bottom (*f*). As shown on the map (fig. 3) all these species, except *hoffmanni* (5), have a very similar distributional range, and the variation in any given locality is parallel. Thus, the color variants (ecogenotypes) of all five species at the northernmost part of the map (top) are of the types *a* or *b* (the darkest) and at the southernmost part (bottom) are of the types *d*, *e* or *f* (the lightest). A comparison with any of the climatic maps or of meteoro-

[9] *To save space, the extremely large number of subspecific, racial and form names applied to these species will not be discussed here. This is likewise true in relation to the other illustrations shown.*

logical data of the region will show that there is decreased solar radiation to the north, increased precipitation and cloudiness to the north, and lower temperatures to the north. There is also increased plant cover on the earth (including darker colored soil) and a higher humidity. From left to right (west to east) on the map, it is seen that the color type is darker on the west and lighter to the east. This is correlated with several factors (compare with climatic or life-zone map): the west is nearer to the ocean and hence there is greater precipitation, higher humidity, more vegetation, darker soil, more cloudiness and cooler temperatures during the growing season (air mass movements are prevailing from west to east). Specifically, several points should be noticed. At San Francisco on the coast, species 1, 2, 3, and 4 are represented by their ecotypes *a* or *b*. About twenty miles inland, still in the coast range, three of these same species are represented by their ecotypes *b* only. In southern California, the effect of the coast is most pronounced. At latitude between 34° and 35°, longitude 120° the species 1, 2, and 4 are represented on the coast by the genotypes *a*, *b*, or *c*, inland thirty miles by *c*, *d* or *e* and still farther by *f* in one or two species. (The distributional data on several of these species are much more detailed than could be represented on a map of this scale.) The effect of increase in elevation is shown in the Sierra Nevada mountains at latitude 37° or 38° where at lower elevations, the color ecotypes are respectively *b* or *c*, or *c* or *d*. At higher elevations these are *d*, or *e*, respectively. The effects of a desert habitat with little precipitation, little humidity, little vegetation and high solar radiation can be seen everywhere in the Mohave desert and the area east of the Sierra Nevada mountains. Ecotypes in this area are from *d* to *f*.

The illustrations (fig. 4) show series of five species of *Argynnis* within the state of California (one species has two isolated clines or variation gradients and is therefore shown twice). Column (1) is the Coast Range cline of *callippe*, column (2) is the Sierra Nevada cline of *callippe*, column (3) is *monticola*, column (4) is *montivaga*, column (5) is *adiaste* and column (6) is *zerene*. As shown on the map (fig. 5), the variation of all these species is from north to south. In the north there is an increase in the *Group One* pigments and a decrease and darkening of *Group Two*: the reverse takes place to the south (ecotypes *a*, *b* in the north and *d*, *e* in the south). It should be stated that since these species seem to be limited usually to a single life-

zone, the elevation at which they live in the south is higher than the elevation in the north. Also the country is more arid, lighter in color and with less vegetation. *Argynnis callippe* along the coast of California is darkest at localities closest to the sea and increasingly light in color inland. The locations of the populations and the colors which they possess can be closely correlated with the landward extensions of the costal fogs. (See at San Francisco, *a* on the coast and *c* inland.) The illustrations (fig. 6) show two species of *Argynnis* (*Brenthis*) from two localities, shown here to illustrate this same sort of variation in localities away from the Pacific Coast, one father south, more inland and at a higher elevation than the other. Specimens (*a*) of both species are from Colorado, (*b*) from the northeast (Newfoundland and Labrador respectively); (*c*) and (*d*) are the same specimens as (*a*) and (*b*) but illustrate the ventral surface of the wings rather than the dorsal. An increase in *Group One* and a decrease and darkening of *Group Two* colors is present in the material from the northeast as compared to the Colorado material. It is seen that the variation takes place on both surfaces of the wings, as it also does in all the other species described.

The Family Satyridae.—Three species of the Satyridae are shown in the illustration (fig. 7). These species were selected especially to show the variation in *Group Two* pigments; *Group One* pigment varies also in many races but is not shown here, The species shown are (1) *Oeneis nevadensis,* (2) *Coenonympha tiphon* and (3) *Oeneis chryxus.* The colors of the wings are from a rufous color in the dark individuals at the bottom (*d*) to the very light (almost white) individuals at the top (*a*). Each of these species is so closely parallel to the other in color that of the three species, there appears to be no difference in the ground color when individuals of the same letter are compared (1*a* to 2*a* to 3*a*, etc.). *Oeneis nevadensis* variation is quite similar geographically to the preceding — dark in the north and light in the south. The species ranges from British Columbia to Mendocino county, California; (*d*) is from the northern locality, and (*a*) is from the most southern locality. *Coenonympha tiphon* is a species which has considerable variation throughout the western and northern parts of North America both in relation to *Group One* pigments and to *Group Two* shown here. In general, there are more races with much of *Group One* pigmentation and dark *Group Two* pigmentation in the north and the reverse in the south but this ideal situation is broken up by local influences.

The species habitat is in grasslands and it would appear that this exerts a great influence on the coloration of the butterfly. In the Northwest where the grass is mostly evergreen the butterfly is darkly colored, as it is also in the high mountain meadows of eastern California and Nevada. In the light-colored, dry-grass hills of California and southern Oregon, however, the species has the very light color shown in the figure (*2a*). There seems to be little other reason for this entire area being populated with a light form; chance seems doubtful for the same reasons as given in the former paper on *Oeneis chryxus* (Hovanitz, '40*a*). The dry grass does make a remarkably light-colored background just as does the white granite rock in the Sierra Nevada. *Oeneis chryxus* is also locally variable according to the color of its habitat, though it, too, is darker in the north than in the south in general — this darkness being due to the increase in *Group One* and in the darkening of *Group Two* pigments. The butterfly, in California at least, is light colored in areas of light-colored ground cover and dark in areas of dark-colored ground cover. A detailed discussion of the variation of this species in California has been given in Hovanitz ('40a) and will not be repeated here.

The Family Lycaenidae.—The illustration (fig. 8) shows two species of the Lycaenidae, *Plebejus icarioides* (1) and *Glaucopsyche lygdamus* (2) with a range of variation from an almost total lack of black pigmentation in the spots to a very heavy deposit. The amount of the black melanin in the spot (*Group One*) varies in the given regions and conditions in the same way as the black pattern bands in the other families. In the north there is an increase in the size of the spots; at high elevations in sand-dune areas and in desert areas the spots decrease in size. The San Francisco sand dunes are striking in the fact that at least three local races of different lycaenids (*P. icarioides, G. lygdamus,* and *Callophrys dumetorum*) all have developed races here with extensive white spots of a degree nowhere else attained. Figures (1a) and (2a) show white-spotted races of two of these species. Besides developing the white race in the one locality at San Francisco, *P. icarioides* has also lost its black spots in the sand dunes at Vancouver Island, at Pismo Beach (in Southern California) and along the white granitic area of the desert on the eastern side of the Sierra Nevada mountains. In addition to the variation in the deposition of *Group One* pigment in the spots on the under side of the wing, many forms show variation in the deposition of an orange pigment along the

borders of the wings on the upper side. The series illustrated (fig. 9, column 1) shows the variation from the form with the greatest quantity of *Group One* pigment to the form with the greatest quantity of *Group Two* pigment. The *Group Two* pigments also become lighter in color. The species is *Plebejus saepiolus* which in California occurs in the Canadian and Hudsonian life-zone meadows of the Sierra Nevada and southern California mountains. As shown on the map (fig. 10) the variation is from an increase in *Group One* pigment in the north to an increase and lightening of the *Group Two* pigment in the south. Besides the differences in the physical characteristics of the environment due to the different geographical position, the populations in the south are at a higher elevation than those in the north and there are fewer cloudy days in the south than in the north.

The Family Riodinidae.—Only one species of this family (*Apodemia mormo*) is wide-spread in western North America. The pigments of the family seem to be homologous with those of the Nymphalidae and the Satyridae. In the far north (Washington), the representative form (*mormo*) has an increase in black pigmentation (*Group One*) and a darkening of the rufous pigment (*Group Two*) (fig. 9, column 2). In the south, these are reversed (the races *mexicanus, virgulti* and *deserti*). In California, coastal populations have an increased percentage of melanin as compared to inland ones and populations in the desert have the reverse of those in areas of greater precipitation. In the granitic area of the Sierra Nevada mountains a race with an increase and lightening of the rufous coloration (*Group Two*) and decrease in the melanin coloration (*Group One*) is present.

Butterflies Having Pigments of Groups One, Two and Three

The Family Pieridae.—Three genera of this family are of common occurrence in the western parts of North America, *Colias, Pieris* and *Anthocharis.*[10] The species of *Colias* are in such an unstable taxonomic state that it is difficult to describe the color variation and distribution and at the same time always be sure that one is remaining within the same interbreeding unit or species. *Colias* does not form local differentiated races of as small an area as many of the species above described but any given form seems to occupy a larger geographic area; this is perhaps related to the more far-flying habits of the species. Any

[10] *On account of poor black-and-white rendition of the colors of these groups, no illustrations of pigment Group Three are shown.*
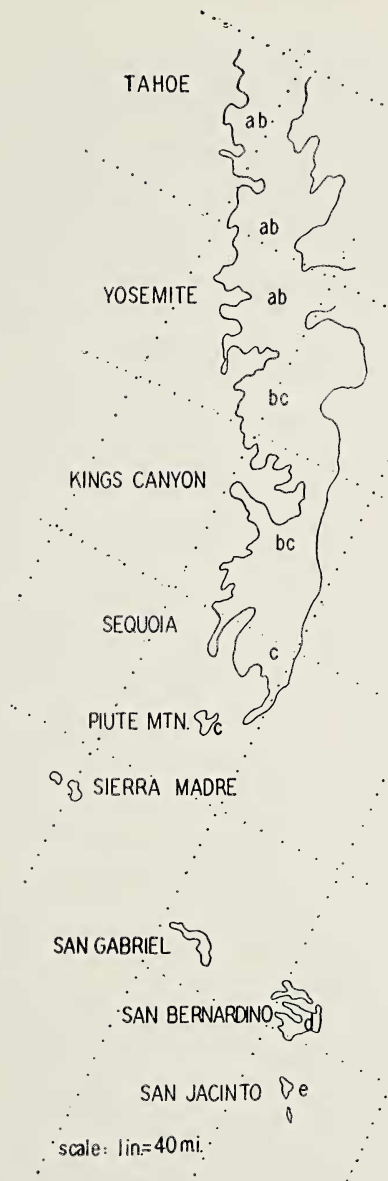
Fig. 10.—Map showing the distribution of *Plebejus saepiolus* female color variation in the California mountains. The line encloses the approximate inhabitable territory of the species from the north near Lake Tahoe in the Sierra Nevada mountains to the south in the San Jacinto mountains. The letters refer to areas where populations exist having butterflies of the same type as those designated by the same letter in figure 9, column 1. These show only representative populations, *not* all those known.

given geographical color form, therefore, must be compared to the climatic characteristics of a larger area instead of a small one. Of the three ground colors of this family (white, yellow and orange of *Group Three*), races with white color seem to be commoner in the far north and orange races in the far south. Yellow races are most abundant in the intervening territory. Areas with warm winters seem to have orange forms prevalent (the Pacific Coast and tropical areas) while the yellow and white forms are commonest in areas having cold winters (polar areas and the northeast Atlantic coast). Spring and autumn generation forms of this genus (*ariadne, autumnalis, vernalis,* etc.) have an increase in black (*Group One*) pigmentation and a decrease in orange (*Group Three*) pigmentation. Several species of *Pieris* exist in North America but the one species *Pieris napi,* will be used here to illustrate the types of variation in this group. In arid parts of the species' range, the intensity of black pigmentation upon the wings is greatly reduced (*castoria,* etc.) (fig. 11, column 3). Such forms occur in the southwestern United States at least in the summer generation. In the far north (Alaska), the forms (such as *pseudobryoniae*) have an increase in the black pigmentation as shown in the illustration (fig. 11, column 1). In the spring form in the south (*venosa*), the pigmentation is also greatly increased (fig. 11, column 2). In some of the arid mountain ranges of the Great Basin, the only yearly generation has a reduced amount of this pigment. In many summer forms and summer generations, there is present a suffusion (*flava*) on the upper surface of the wings of a yellow color (*Group Three*) which is less often found in the spring form. *Anthocharis* illustrates better than *Pieris* and *Colias* the variation in this family. It has present all three groups of pigments whereas the latter have only two. The orange or red apex spots of this genus represent *Group Two*-subgroup *c* pigments. In Alaska, a form with a very dark-red apex spot, an increased amount of black pigment and a white ground color occurs. In the south (California), the summer forms have a smaller and lighter apex spot, less black pigmentation and an increase in a yellow ground color suffusion in the area of the white (*sara*). In arid Utah, the only yearly generation of this species (*brouningi*) has a small, light-red apex spot and a reduction of black pigment of a degree no where else attained. The spring generation of the species in coastal California (*reakirti*) has a greater amount of black pigmentation and few-
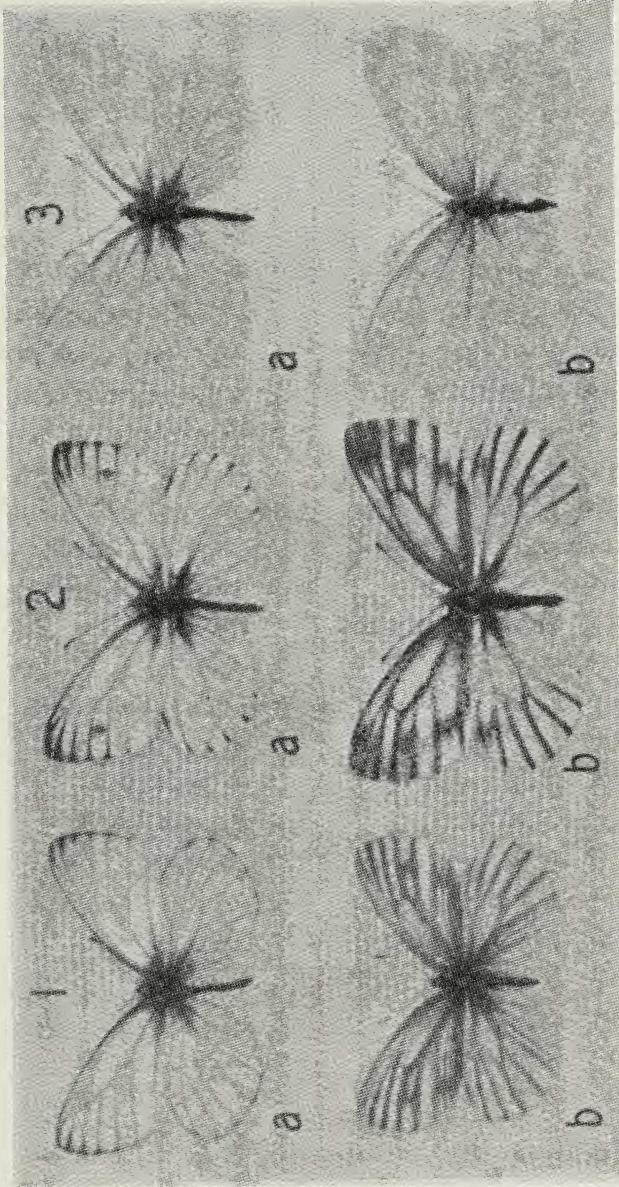
Fig. 11.—Variation in *Pieris napi*. 1. Alaskan form, (*a*) male, (*b*) female. 2. Spring generation form from central California, (*a*) male, (*b*) *female*. 3. Summer generation form from central California, (*a*) male, (*b*) female.

er yellow pigmented individuals than the summer generation in the same place. A form in the high Sierra Nevada mountains (*stella*) which exists in the white granitic areas is always yellow in color. In the closely related species, *cethura*, the ground color is yellow in Arizona (*pima*) and white in California (*cethura*). In the Mohave desert of California, a form (*deserti*) occurs in which there is a complete loss of the orange tip (*Group Two*) from the apex of the wings and a reduction in the amount of black (*Group One*).

The Family Papilionidae.—In the two genera of this family, there are present all three pigment groups. In *Papilio,* there are few examples of the ecological variation because the species are rather far-flying and not very variable locally. *Papilio eurymedon* shows some variation. In a British Columbia form, the pattern pigment (*Group One*) covers more area than the form in the lowlands in California, though a forest form of the California mountains (*albanus*) has again an increase in the *Group One* pigment. This dark California form does exist at a higher elevation than the lighter form but this seems to be correlated to the forest habitat of the dark one. *Papilio rutulus* varies little in *Group Two* pigments but does develop a form in the southwestern semi-arid regions in which the yellow ground color (*Group Three*) becomes more orange in tint. In the north it is pale yellow. The eastern *turnus* seems to produce such an orange form in the southern parts of its range. In the north, these forms develop an increase in the black pattern elements (*Group One*) and a lighter yellow-ground color (*canadensis*) (*Group Three*). In the genus *Parnassius*, both widely distributed North American species (*clodius* and *smintheus*) develop races with an increase in melanin pigmentation (*Group One*) and a darkening of the red spots (*Group Two* subgroup *c*) in the far north (*claudianus,* etc.). In the southern and arid parts of the ranges of these species, the *Group One* pigments are decreased and the *Group Two* pigments are a paler red or orange color (*altaurus,* etc.).

DISCUSSION

Parallel variation in the morphology, color and physiology of non-interbreeding organisms has been observed in several major groups of animals and plants. There appears to be, however, no one source where all the evidence in these divergent fields has

been summarized or reviewed. Reinig ('37) gives the best recent summary of the work dealing mainly with the color variation in European Lepidoptera. He appears to consider the genetic, the physiological and the ecological evidence but does not make any conclusions as to a correlation between the color types and any specific environmental factors. However, he includes a rather extensive bibliography on the earlier work in the field; this will not be repeated here. Recent treatises on evolution by Goldschmidt ('40) and Dobzhansky ('37) as well as the volume on ecological animal geography by Hesse, Allee and Schmidt ('37) also touch on this field in their reviews of the literature. Parallel variation in plants has been extensively covered by Turesson ('22 and '30) and Clausen, Keck and Hiesey ('40) in relation to the influence of the environment. Vavilov ('22) has formulated the "law of homologous series in variation" on the basis of parallel variation in plants though he does not bring adaptation into his discussion. Work in closely related fields (not in butterflies) may be mentioned by referring to the work of Dice ('40a) and Sumner ('32) on rodent ecotypical coloration (*Peromyscus*), Alpatov ('29) on the geographical races of the honey bee (*Apis*), Tower ('06, '18) on the color variations in the potato beetle (*Leptinotarsa*), Allen ('74), Beebe ('07) and Rensch ('29, '36) on the variation and distribution of birds in relation to color, Enteman ('14) on coloration in wasps (*Polistes*) and Dobzhansky ('33) on parallel color variation in ladybird beetles (Cocinellidae). Much of the work done on mimicry in butterflies should probably also be mentioned here as perhaps being in many cases only parallel ecological variation causing convergence of color pattern appearance (Punnett, '15; Poulton, '08, '09, '31; Wallace, '71; Heikertinger, '33-'36; Eltringham, '10). The regional or local area mimicry would also belong in this class.

Vavilov (as mentioned above) described the remarkable regularities in variation existing between various species of plants and thereby formulated his "law of homologous series in variation." He thus showed that homologous and analogous variations in different species are of common occurrence. The intensive and extensive work of the *Drosophila* school of geneticists has provided excellent material for the study of homologous gene mutants in different species (Sturtevant, '40), an amount of work which could hardly have been accomplished with any other animal. Definite genetic evidence is now accumulating to prove the commonly accepted idea that closely related species may be very similar in genetic constitution and that genes having similar action upon the pheno-

type of the animal may be homologous in the different species. The importance of this fact to parallel variation is that these mutants should tend not only to produce varieties within the different species having similar phenotypes, but also, if these homologous mutants gave a survival advantage to the phenotype of the possessor under a similar set of environmental conditions there should come about as the result of natural selection parallel and homologous series of variation. It should be realized, however, that *different* genes can give *identical* physiological effects. Besides genetic homologies, direct physiological homologous effects upon the phenotype of an organism can be produced by the direct action of similar environmental conditions (Goldschmidt,'38, Harrison, '32, Harrison and Garrett, '26, Allee and Lutherman, '40, Gerould, '16, Standfuss, '98, etc.). In most cases where one is dealing with wild populations, the effects of the environment and the effects of the genom may be difficult to differentiate without laboratory analysis, and these two effects may also be additive in their phenotypic expression. (See Turesson ('22).) This is especially the case where a single species varies seasonally as well as geographically. In the discussion of parallel variation above no attempt has been made to give a clear separation between hereditary, parallel, color variation and the environmentally modified variation though in many cases experimental evidence is available to suggest such a differentiation. A great deal of work has been done by various experimenters on the direct physiological effects on color of temperature, humidity, and to a lesser extent, light. It is generally agreed that lower temperature, higher humidity and a lower intensity of light [11] are conducive to the production of a greater quantity and a darker quality of the pigments on butterflies which fall in the first two groups given in the preceding sections (for reviews, see Chapman, '31 and Reinig, '37). These physiological results are therefore in complete agreement with the zoogeographical and ecological results developed in this paper.

The non-acceptance of the theory of the inheritance of acquired characters makes it a more difficult problem to explain the genetic, parallel color variation of this type on the same basis. It becomes necessary to prove that a particular color variety is better adapted or fitted to a given environment and therefore has a better survival value or reproductive advantage over other types under the same

[11] *The complete absence of light is, in many cases, accompanied by a reduction in pigment formation and deposition.*

conditions. This proof has never been obtained under natural conditions. It has, however, been suggested many times and must be considered as being an unproven but highly probable hypothesis. Kühn and von Engelhardt ('37) have shown that a genetic mutant of a moth which has as a phenotypic character the suffusion of the wings with melanin pigment (*Group One*) has an increased viability under conditions of lower temperature and increased humidity than the same moth without the single mutant effects. It has also a slower genetic development rate which would seem to fit in with the longer development time usually possible under these environmental conditions. This study is perhaps the nearest approach to proving how a genetic melanic mutant might be better adapted to living under the accompanying environmental conditions that has ever been made.

It seems that none of the theories of genetic melanism (increase in *Group One* pigment) in animals in the industrial centers of the world (see Hasebroek, '34 for review) have as yet been found to be entirely successful. The suggestion may be made here that perhaps the cause of the increase in melanic forms in these regions is not to be found in the direct effects of the industrial material with which the air and vegetation of the areas are contaminated (such as smoke, soot, chemical vapors and deposits, etc.) but rather may be looked for in the indirect effects of these in reducing the light and direct heat penetration of the atmosphere and in the greater absorption of that which does penetrate it. The effects of continued dust in the air are very likely to be similar to those produced by fog and clouds; city air contamination is high and the effect on light penetration is great (see Brackett, '37). Considering the matter in this way brings the problem of industrial melanism closer to the essentially similar natural "melanism" described above; these two problems may have the same basic foundation in ecology and population genetics. What remains to be proved in any case is the physiological fitness of one type over another under these essentially similar environmental conditions. Ford's theory ('37, '40) of industrial melanism appears no closer to proof than any of the others. He suggests that mere selection of dark forms over the light could not explain the melanism but instead that the dark forms (when the melanic gene is dominant) are naturally hardier than the light forms throughout the range of the species. They are selected against because they lack cryptic coloration, except in industrial areas where the advantages of

hardiness overrules the advantages of cryptic coloration. The author does not see how this clears up the problem since it still leaves an unknown advantage to be conferred on the melanic forms in industrial areas. The variation of butterfly pigments in relation to the physical environmental factors seems, according to all experimental evidence, to be too great to have much effect on cryptic coloration. The variation of *Group Three* pigments is irreconcilably opposed in "protectiveness" to the pigments of the other groups. In light-colored habitats, *Groups One* and *Two* become lighter in color but *Group Three* becomes darker. Certainly this is no adaptation in the sense of cryptic coloration, though there seems to be no doubt that there is adaptiveness involved somewhere in the developmental physiology of the butterfly. No doubt, too, in the case of some species and especially in the case of larvae that feed in the daytime, protective coloration does lead to a differential selection of colored types. This is, however, not the place for an extended discussion of the merits of "protective coloration" (see Cott, '40, for review); it is intended only to suggest that good theory firmly established as dogma should not be put up as a wall to block efforts to find new scientific facts.

Dice ('40b) correlates the pelage color of a deer mouse (*Peromyscus maniculatus*) across North Dakota with the environmental variation across the same terrain. He finds a gradation in pelage color from light-colored in the west to dark-colored in the east and correlates this with a lighter soil cover in the west than in the east. Also, there is present an increase in elevation, a decrease in precipitation and a more arid character of the vegetation in the west as compared to the east. These results may be compared with those presented in this paper. The data of Benson ('33), Dice and Blossom ('37) and Hovanitz ('40a) in which animals possess a body color (or wing color) closely similar to the substrata on which they live can also be related in the same way, though in these cases soil color seems to be the only variable. Dice ('40) presents evidence derived from variation in small animals that pelage color is almost always variable in direct relation to the color variation of the soil habitat. He shows that similar color races may be developed at isolated points if the environmental conditions are parallel at those places; he also concludes that the subspecies is primarily an ecologic unit. Essentially these same conclusions have been arrived at and put into modern eco-genetic terms as early as 1922 by Turesson (already mentioned). The present author believes that they are true also for butterfly variation, though he

would include not only the subspecies but the species as well, thus bringing in Darwin's "Origin of Species by Natural Selection."

The only rule of color variation definitely formulated in the literature is known as Gloger's (cf. Rensch, '36). This states that in warm-blooded animals, races living in warm and moist regions have more melanin pigmentation than races living in cooler and drier regions and that races inhabiting arid, desert regions have more yellow or reddish pigmentation. The rule was found to hold in a significant number of cases although there were exceptions. In insects, various authors (Dobzhansky, '33; Reinig, '37; Hesse, Allee and Schmidt, '37; Enteman, '04) produce or review evidence leading to rather diverse opinions on color variation, but in general seeming to agree that darker pigmentation increases under humid and cool conditions, and that the lighter pigments increase under dry and hot conditions. This is not exactly the order in which the pigmentation variation takes place in warm-blooded animals but it is suggestive of the same trend. Obviously, the physical conditions (temperature and humidity) do not vary together but rather do so mostly at random (though not always), the result being visible in the diverse climates of the hot, humid tropics, the hot, dry tropical deserts, the cold, humid arctics and the cold, dry arctics. Many apparent exceptions and reversals of the rule are therefore to be found depending on the particular group being studied. Many authors (cf. Dobzhansky, '33 and Enteman, '04) have used such terms as "centers of light forms" and "centers of dark forms" to describe the parallel color variation found since this does not make necessary an interpretation of the physical and biological factors involved in the variation. These centers of pigmentation are shown to be centers of certain physical conditions such as aridity, high temperature, etc., though they might, more specifically, have been said to be centers of low precipitation, low humidity, high temperature, high solar radiation, fast animal development and light colored soil.

CONCLUSION

It may be concluded that butterfly color variation is closely correlated with the variation in the environmental conditions. Because most subspecific color variations found in the wild are genetic, the type of variation may properly be termed ecogenotypic (after the terminology of Turesson). As many of the color variations are not protective or "adaptive" in themselves, it is believed

that the colors are only a secondary product of some physiological change in development, metabolism or "hardiness" which are of primary adaptive value. It is believed that proof of any theory of adaptive coloration must be accompanied by proof of the mechanism of the selection and this proof has not yet been presented for any phase of the problem.

Four environmental conditions are found to be of significant interest in the correlations with pigment color variation: increase or decrease in temperature, increase or decrease in precipitation or humidity, increase or decrease in solar radiation and rate of development of the organism.

SUMMARY

1. The pigment colors of North American butterflies are divided into three basic groups for comparing their variation with the variation of the environmental conditions. These are: *Group One*: the black, brown and gray melanin pattern elements found in all families, *Group Two*: the tawny, rufous, red, orange and yellow colors with a brown tint which form the ground colors in the Nymphalidae, Riodinidae, Satyridae, Lycaenidae, Danaidae, and the Libytheidae; also the yellow and white colors of these six families and orange and red spots of the Pieridae and the Papilionidae, and *Group Three*: the white, yellow and orange ground color pigments (pterines) of the Pieridae and the Papilionidae.

2. The variation of each of these three pigment groups is correlated with certain geographic regions and conditions in which the insects live. It was found possible to correlate lower temperature, increased humidity, increased precipitation, decreased solar radiation, and decreased development rate in most cases with the following pigment changes: *Group One* pigments increase in area and intensity on the wing, *Group Two* pigments increase in intensity or darkness and may decrease or increase in area and *Group Three* pigments show increased development of the lighter of the three pterine pigments (white, yellow and orange).

4. The conclusion is reached that these factors play an important part in the color variation of butterflies and that, therefore, the color variation may be considered adaptive.

5. It is also concluded that contrary to established dogma, the adaptiveness of animal coloration need not only be "protective" but may be only a secondary product of a more fundamental function in the physiology of the animal.

6. Correlations of butterfly color variation with evidence from other animals is given to show the parallelism in the variation and in the ecological characteristics of the environments.

ACKNOWLEDGMENTS

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